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Update on the distribution of *Isaurus tuberculatus* Gray, 1828 (Cnidaria, Zoantharia) and first insight into the microanatomy and cnidom of South Atlantic populations

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Abstract

The zoantharian *Isaurus tuberculatus* Gray, 1828 is highly variable in its morphology, and considered pantropical. As it is a shallow water and zooxanthellate species, its wide distribution has been questioned, and it is likely that the Atlantic and Indo-Pacific populations are distinct species. Here we update the distribution of this species in Brazil and provide the first description of the microanatomy and cnidom of populations in the South Atlantic. Along the Brazilian coast, the species is distributed from Ceará to Bahia, and is also in the Fernando de Noronha archipelago.

Keywords

Brazil, Cnidae, Zoanthidae, Zoanthidea

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Introduction

The genus *Isaurus* Gray, 1828 (Zoantharia: Zoanthidae) is characterized by zooxanthellate, recumbent (non-erect) polyps with no mineral incrustations on the column or the coenenchyme (Low et al. 2016). *Isaurus tuberculatus* Gray, 1828 is the type species of the genus, described from museum material of unknown origin. Over 20 species have been ascribed to this genus (Fautin 2006; Low et al. 2016), but only three are currently recognized as valid: *I. tuberculatus* (pantropical), *I. maculatus* Muirhead & Ryland, 1985 from Fiji, and *I. cliftoni* (Gray, 1867) described for Western Australia and Fiji (Muirhead & Ryland, 1985; Reimer and Sinniger 2022).

Four *Isaurus* species were synonymized with *I. tuberculatus*: *I. duchassaingi* (Andres, 1884) (Caribbean), *I. spongiosus* (Andres, 1877) (East Africa), *I. asymmetricus* Haddon & Shackleton, 1891 (Australia), and *I. elongatus* Verrill, 1928 (Hawaii) in the last revision of the genus (Muirhead and Ryland 1985). These species were

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previously differentiated based on size, quantity, and distribution of tubercles, as well as polyp size and subtle differences in cnidae size. However, high intraspecific variability in morphology, according to local conditions, and an overlap of measurements among these species are apparent. Thus, Muirhead and Ryland (1985) argued that there was no justification for keeping the taxa separate.

This synonymization resulted in a pantropical geographic distribution of *I. tuberculatus* extending in the Pacific from Hawaii to Perth (Western Australia), and in the Atlantic northwards to Bermuda (Muirhead and Ryland 1985). Since Muirhead and Ryland's (1985), many new locations in the Atlantic have been reported: Ascension Island (Brown et al. 2016), Brazil (Grohmann and Peixinho 1995; Soares et al. 2011; Santos et al. 2016; Gondim et al. 2020), Canary Islands (Riera et al. 2014; López et al. 2019), Cape Verde (Reimer et al. 2010), Cuba (Varela et al. 2002; Diez and Campos-Castro 2016), Curaçao and Saint Eustatius (Montenegro et al. 2020), Saint Helena (Santos et al. 2019), Florida, USA (Reimer et al. 2012), Caribbean Colombian and other areas in the Caribbean (Acosta et al. 2005), São Tomé and Principe (Wirtz 2018), and Mexican Caribbean (Fautin and Daly 2009). In the Indo-Pacific, additional locations have been reported from Palau (Santos and Reimer 2018), India (Khushali et al. 2014; Kumari et al. 2017), Taiwan (Reimer et al. 2011b), Hawaii (Forsman et al. 2012), Vietnam (Reimer et al. 2015), Indonesia (Sinniger et al. 2005), New Caledonia (Laboute and Richer de Forges 2004), Moluccas and Lembeh Strait (Reimer et al. 2014), Gaum (Paulay et al. 2003), and Japan (Reimer et al. 2008a), and in the Indian Ocean, from the east coast of South Africa (Risi 2014; Risi and Macdonald 2015). The global distribution of the species can be accessed through the World Register of Marine Species at https://www.marinespecies.org/aphia.php?p=taxdetails&id=101058.

Curiously, many of these authors affirmed that this species was easily identified by the presence of tubercles and curved polyps or by the comparison of molecular sequence data with material from Japan, previously identified as *I. tuberculatus* (e.g., Reimer et al. 2012; López et al. 2019; Santos et al. 2019). However, complete morphological or microanatomical descriptions of specimens were lacking in these studies, which do not contribute much to the understanding of the morphological variation in *I. tuberculatus* or the delimitation of species within the genus (e.g., Grohmann and Peixinho 1995; Varela et al. 2002; Brown et al. 2016).

The wide distribution of *I. tuberculatus* has been attributed to Zoanthinae larvae (typical of the family Zoanthidae) having a long planktonic stage, up to 190 d (Polak et al. 2011). However, this has been reported only in *Palythoa tuberculosa*, the most widespread species in the Indo-Pacific. *Isaurus tuberculatus* has never been recorded outside of tropical and subtropical zones, which is a common distribution pattern found in zoantharian species associated with endosymbiotic Symbiodiniaceae zooxanthellae (Reimer et al. 2008b; López et al. 2019). Thus, some authors have suggested that Atlantic and Pacific populations are very likely separate species (Reimer et al. 2008b, 2012; Montenegro et al. 2020). Although molecular studies have been carried out with the aim of defining the phylogeny of the genus, the two mitochondrial markers used so far are inadequate to distinguish species within a genus. Furthermore, specific primers for zoantharians from faster evolving markers, such as ITSrDNA, do not work for *Isaurus* (Reimer et al. 2008b; Risi and Macdonald 2015). Therefore, the genus, and particularly *I. tuberculatus* sensu lato, requires a comprehensive revision, which should include a detailed description of the external morphology, microanatomy, and cnidom, as well as the use of other relatively fast-evolving DNA markers, to characterize morphological variation among populations.

Here, we update the geographic distribution of *I. tuberculatus* along the Brazilian coast and also describe three populations in northeastern Brazil. The microanatomy and cnidom of *I. tuberculatus* are described for the first time from South Atlantic populations. The potential separation of Atlantic and Indo-Pacific populations as different species is discussed.

Methods

Between 2003 and 2019, several *Isaurus tuberculatus* colonies were collected from three locations along the northeastern coast of Brazil (Fig. 1). Collecting of specimens was conducted under the collecting permit SISBIO 15691-1 obtained from ICMBio, Ministério de Meio Ambiente, Brazil. The colonies were located on coastal reefs in tidal pools in the intertidal zone or in shallow water (<2 m). The region has a tropical climate with a rainy period (March to August) and a dry period (September to February) with annual rainfall varying between 1250 and 2000 mm (Macedo et al. 2004). When possible, the colonies were photographed in the field and 2–10 polyps were collected. Most collected specimens were fixed in 10% formaldehyde, but some were fixed in 70% alcohol for micro-anatomical analyses. All voucher specimens were deposited in the Cnidaria Collection of the Museu de Oceanografia Petrônio Alves Coelho, Universidade Federal de Pernambuco, Brazil (MOUFPE-CNI).

The samples were measured and examined for the external and internal morphology (e.g., color pattern, polyp form, size and distribution of tubercles, number of tentacles, presence of gametic tissue). The cnidom was characterized for at least two individuals from each location. Measurements of cnidae were made from preserved material; small pieces of tissue were smeared on slides and examined using a microscopy at 1000× magnification. We scanned through the slides and haphazardly chose 20 capsules of each type (when possible) to measure to generate a range. The classification follows Schmidt (1974) and are presented as range, mean, and standard deviation. The histological process follows the

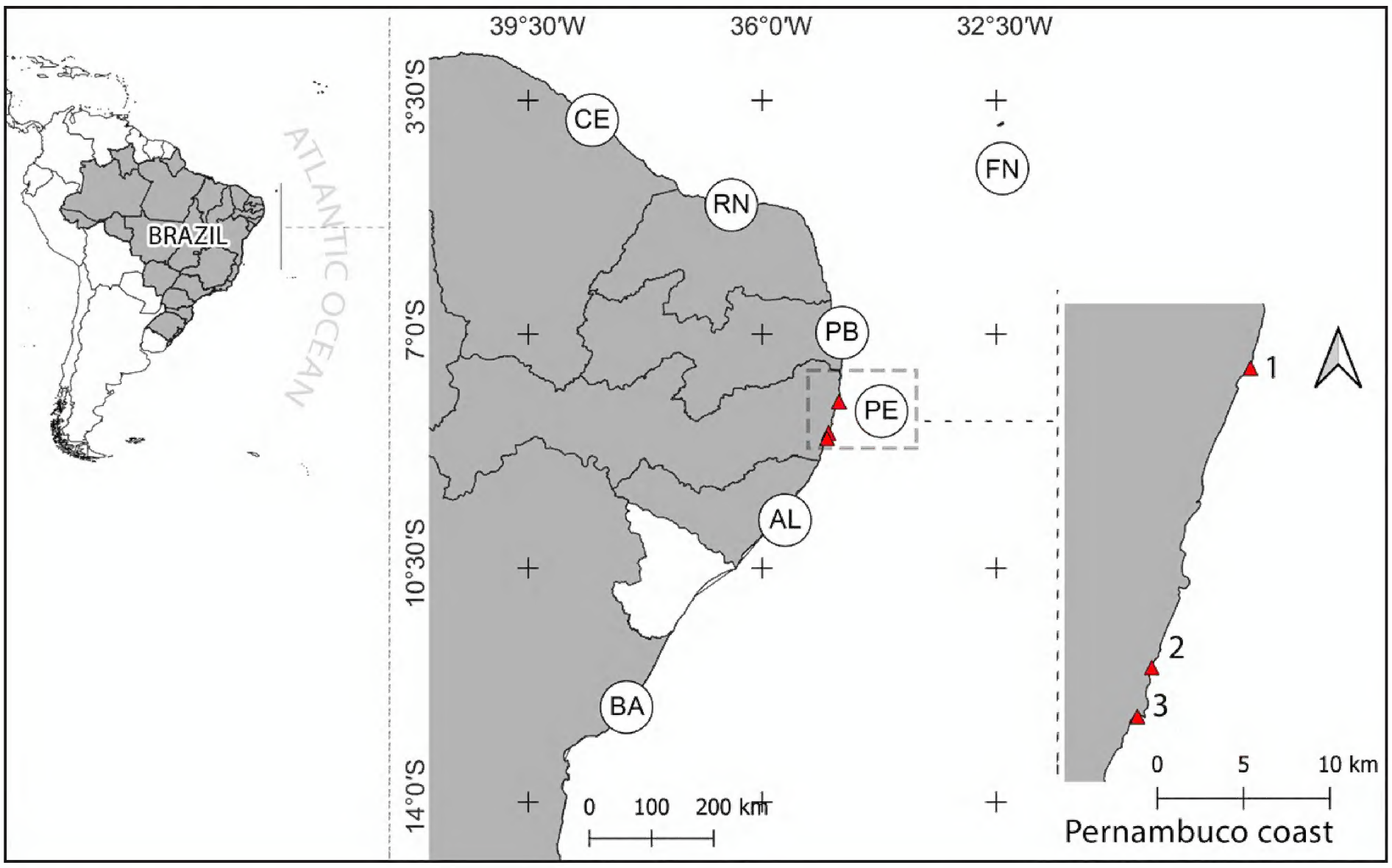

Figure 1. Distribution of *Isaurus tuberculatus* along the Brazilian coast and location of studied populations. Black circles = previous published records; gray circles = previous unpublished records (gray literature); red circles = new records, studied populations. Abbreviations and sources of data: CE = Ceará (Morandini et al. 2006; Rabelo and Matthews-Cascon 2007; Soares et al. 2011); RN = Rio Grande do Norte (Gondim et al. 2020); FN = Fernando de Noronha Archipelago; PB = Paraíba (Gondim et al. 2020); PE = Pernambuco (Laborel 1970; Gondim et al. 2020); AL = Alagoas (Gondim et al. 2020); BA = Bahia (Grohmann and Peixinho 1995; Gondim et al. 2020).

pattern for Zoantharia (Swain and Swain 2014) and the slides (7–8 µm) were stained with hematoxylin-eosin stain.

We also gathered data on the external morphologies of other populations along the Brazilian coast and compared these with previously published data on *I. tuberculatus* in other locations throughout its distribution global area. All the currently accepted synonyms were considered (following Muirhead and Ryland 1985). To update the distribution of *I. tuberculatus* along the Brazilian coast, all the literature, including gray literature (conference abstracts and theses) was reviewed. Only material recorded, confirmed, or identified by specialists in Anthozoa was used.

Results

***Isaurus tuberculatus* Gray, 1828**
Figures 2, 3, Table 1

Synonym list. See Muirhead and Ryland (1985). We consider *I. tuberculatus* (sensu lato) to include all the currently accepted synonyms for the species, based on the article by Muirhead and Ryland (1985) and the most recent revision of the genus (Reimer et al. 2008b).

Material examined (New records). BRAZIL – **Pernambuco** • Porto de Galinhas; 08°33′33″S, 034°59′00″W; 2 m; 9.VI.2001; C.D. Perez leg.; MOUFPE-CNI 921 – **Pernambuco** • Guadalupe; 08°37′48″S, 035°07′30″W; 1–2 m; 4.III.2003; D.A. Vila-Nova, C.D. Perez leg.; MOUFPE-CNI 922 – **Pernambuco** • Serrambi; 08°33′S, 35°01′W; intertidal; 19.IV.2014; P.B. Gomes, C.D. Perez leg.; MOUFPE-CNI 923.

Diagnosis. *Isaurus* with varying number of characteristic large tubercles over the body surface. Polyps lacking tubercles occur uncommonly amongst those, presumably clone mates, having the usual distribution of tubercles. Crown tubercles (Larson and Larson 1982) forming a characteristic and definite edge to the capitulum; body tubercles usually arranged in longitudinal series (according to Muirhead and Ryland 1985).

Identification. We identified our samples as *I. tuberculatus*, although there is much variation in size, coloration, and tubercle distribution between locations, colonies, and polyps of the same colony. There is a large overlap in the measurements, without clear differentiation between populations. Thus, the description will be presented as a set, joining all populations and highlighting the most notable differences, when present.

Colony descriptions. All the collections were carried out during day and the polyps had retracted tentacles in the typical posture, bent parallel to the substrate, as described for *I. tuberculatus*, (Fig. 2A–D). The polyps were attached with a thin coenenchyme, but individual polyps were also observed.

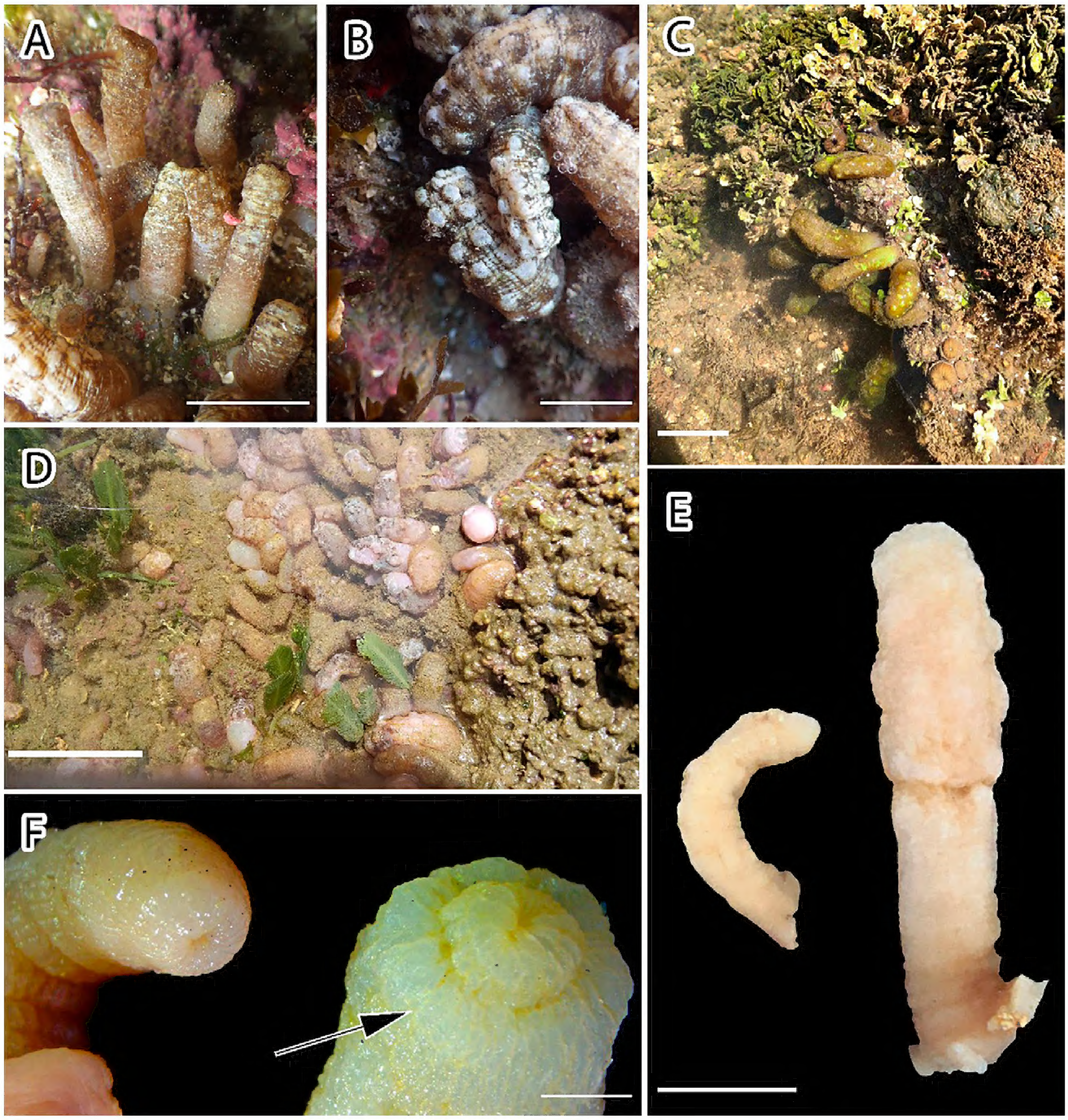

Figure 2. Variability of *Isaurus tuberculatus* colonies in populations in northeastern Brazil. **A–D.** Samples from Serrambi. **E.** Morphological difference between Serrambi (smaller) and Guadalupe (larger) samples. **F.** Detail of the tubercle crown in a sample from Guadalupe. Scale bars: A, B, D = 20 mm; B, E = 10 mm; F = 5 mm.

In Porto de Galinhas the colony was composed of 15 polyps unconnected or loosely connected by coenenchyme. The greenish-gray polyp coloration was mixed with the background. The colony was on the inner reef border and polyps were fixed in an area near the sandy bottom. The Guadalupe colonies were larger (between 13 and 25 individuals) and very close to one another. The recumbent, non-erect polyps overlapped, creating a tangled appearance. The polyps were fixed in a reef plateau or on the inner edge, in shallow areas (between 1.5 and 2 m). The polyps were brown or cream colored, the smaller ones presented a lighter coloration. In Serrambi a greater variety of colonies was observed. For some, their size and appearance were similar to the colonies in Porto de Galinhas and Guadalupe, but they had over 50 polyps (Fig. 2A, B, D). Only one colony was smaller and was fluorescent green with approximately 12 polyps (Fig. 2C). It was attached in tidal pools in the reef plateau in the intertidal zone.

External morphology. Polyps were 1.0–4.5 cm long (Fig. 2E), 0.3–0.8 cm in diameter at the base, and 0.3–1.0 cm in diameter at the capitulum. When fixed, all the polyps were yellow-cream-colored with paler tubercles. The column presented concentrated tubercles, mainly in the dorsal region. Some polyps also presented tubercles in the ventral portion, but in lesser quantities. In all the colonies, there were smaller, generally paler polyps with

Table 1. Morphological data and size range of length and width (µm) of the cnidae of *Isaurus tuberculatus* in Pernambuco (northeastern Brazil) and other locations in the world (according to Muirhead and Ryland, 1985). * = visible in only one specimen; ** = cnidom not available; † = as microbasic mastigophores; ‡ = as microbasic p mastigophores; § = as rhabdoids.

	I. tuberculatus				*I. spongiosus*		*I. elongatus*		*I. asymmetricus*	*I. duchassaingi*
Locality	Brazil	Townsville	Western Australia	Fiji	Madagascar	South Africa	Hawaii	Hawaii	Vietnam	Belize
Source	This study	Muirhead & Ryland 1985	Muirhead & Ryland 1985	Muirhead & Ryland 1985	Herberts 1972	Carlgren 1939	Walsh & Bowers 1971	Muirhead & Ryland 1985	Pax & Müller 1957	Larson & Larson, 1982**
Column										
Holotrich I	12–16.8 × 6–10.8	22–33 × 10.5–13	22–26 × 6–8	19.1–30 × 6.5–10	16.4–27 × 7.3–9.5	23–32 × 10–12	30–36 × 10–12	22–26 × 6–8	23 × 10	
Holotrich II	23.2–38.4 × 10.8–14.4									
Mesenteries										
Holotrich I	12–15.6 × 4.8–7.2	9–12 × 3–6	10.5–13.5 × 4.5–5.5	8.5–12 × 3–5	9–12 × 3.6–5,4	10–14 × 4.5–5	10–28 × 4–10	10–11.5 × 4.5–5.5	8.5–10.5 × 3.5–5	
b-rhabdoid	12–15.6 × 1.2–3.6									
FILAMENTS										
Holotrich I	12.6–14.6 × 6.5–7.1				31 × 10					
Holotrich II	28–33.6 × 9.2–11.6									
p-rhabdoid B	11.6–14.4 × 3.5–4.8						15–17 × 3–5 ‡			
Spirocyst	26.4–28.2 × 4.8–5*									
b-rhabdoid		11–19 × 3–5	14–18.x 53–5	10.5–17 × 2.5–5	12.7–19.2 × 1.8–4.5†	22–24x3–4 † 4–4.5 × 15.5–19†	19–26 × 3–4	16–18 × 2.5–4.5 §	36	
Pharynx										
Holotrich I	14.6–16 × 5.8–6.5						10–15 × 4–6			
p-rhabdoid A	26.1–28 × 2.9–3.5*						18–23 × 4–5‡			
b-rhabdoid	25.6 –28.2 × 5.2–6	13–17 × 3–5.5	14.5–22 × 2.5–4	15–20 × 2.5–5	13–23 × 2–3.6†	22–24 × 3–4†		17–19.5 × 4–4.5§		
Spirocyst	25.2 × 6*						16–24 × 2–4			
Tentacles										
b-rhabdoid	13.9 (10.4) × 2.4									
Spirocyst	20–3.3	10–19 × 2–3	13.5–16 × 2.5–4.5	12–22 × 2–3	14.5–24.5 × 2–4	14–28 × 2–4	16–26 × 2–4	9–18 × 2–3	19	
Size of colonies	12–50 polyps	NA	NA	NA	NA	NA	Up to 5 polyps	NA	NA	2–200 polyps
Colour	Yellow-cream, brown, green	yellowish-brown;	NA	Green or greyish	NA	NA	Brownish and white, green	NA	NA	Grey-green, brown, yellow
No. of tentacles	34–41	NA	NA	NA	NA	NA	50	NA	NA	38–42
No. of mesenteries	34–42	NA	NA	NA	35–42	NA	Up to 40	NA	NA	NA
Polyp length (cm)	1–4.5	Up to 7	NA	1–4	0.2–3.3	Up to 4	Up to 7	NA	NA	4–5
Polyp diameter (cm)	0.3–1.0	NA	NA	NA	1–7	0.6–0.8	Up to 9	NA	NA	0.6–0.8
Mesogleal tickness (µm)	399–532	NA	NA	NA	300–600	NA	NA	NA	NA	NA

a smooth column and without tubercles (Fig.2F). However, several specimens within the same colony may not present a crown. All the polyps in the fluorescent colony in Serrambi presented tubercles arranged in longitudinal rows, although they formed notable circular rings (transversal rows) around the entire scapus, causing a transversally wrinkled appearance. Some of the Serrambi polyps apparently lack a tubercle crown (Fig. 2E).

Internal anatomy and microanatomy. *Column.* A thin cuticle covers the ectoderm of the column (12–48 µm). Thin ectoderm (52.5–84 µm) discontinuous, forming cellular "islands", separated by mesoglea bridges. Within the islands are ectodermal cells, zooxanthellae (6–8.4 µm), and holotrichs. Thick mesoglea (399–532 µm; Fig. 3A) along the entire length of the scapus; the mesoglea becomes thicker in the region of the capitulum where the crown of tubercles is formed. This characteristic is present in the larger polyps in Porto de Galinhas, Guadalupe and Serrambi. However, the small polyps and polyps of the fluorescent colony in Serrambi present a capitulum without a tubercle crown.

The ectoderm is thicker in the regions next to the tubercle in cross-sections (105–147 µm). In the tubercles only the mesoglea undergoes thickening (maximum thickness 1330 µm; Fig. 3E). In longitudinal sections, on the convex side of the column, the mesoglea has endodermal invaginations resulting in lacunae and canals alternating with the tubercles. Due to these projections, the mesoglea is thinner in these areas (up to 532 µm) of the column. There are no invaginations on the concave side, and the mesoglea has an almost constant thickness. Thin endoderm, simple (12 µm), rich in glandular cells, zooxanthellae and nematocysts.

Tentacles 34–41. Thick ectoderm with epidermal cells, spirocysts, and nematocysts. Mesoglea with many longitudinal fibers and endoderm with many zooxanthellae (up to 9.6 µm) and nematocysts.

Pharynx. Extremely pleated lengthwise. Thick ectoderm with glandular cells and nematocysts. Absence of zooxanthellae. Mesoglea thinner at the siphonoglyph, where the ectoderm is thicker and there are no nematocysts.

Sphincter. Simple but well-developed mesogleal sphincter, occupying almost the whole mesoglea at the distal part. It is only possible to visualize the sphincter of the polyps from Guadalupe and Serrambi (brown colony). Both coincide with the description proposed by Swain et al. (2015), as an orthogonally reticulate mesogleal sphincter muscle. Unfortunately, there was a processing issue with the material from the fluorescent colony in Serrambi and it was not possible to obtain adequate sections for the visualization of the sphincter.

Mesenteries 34–42, with variation within the same colony and between locations. Weak retractor musculature located close to the insertion of the mesentery in the body wall (Fig. 3D). In the mesenteries, cellular islands and rounded lacunae appear in the thickening of the mesoglea. In these lacunae there are large clustered glandular cells. Macroseptum with thin mesoglea, endoderm with glandular cells, spirocyts, nematocysts and zooxanthellae. In the basal part, the septa anastomose and form a network of anastomoses in the center or in the periphery. Filaments provided with glandular and nematocyst cells.

Gametogenic tissue. Only specimens collected in Porto de Galinhas in 2001 presented gametes. The polyps are hermaphrodites (Fig. 3B). The spermatic cysts measure 62.5–103.6 µm (Fig. 3F). Different sized oocytes were visualized on the same polyp, showing asynchrony in gamete development. There were already mature oocytes with a maximum size of 217.1 µm (Fig. 3G).

Cnidom. The samples collected in Pernambuco, northeastern Brazil (western South Atlantic Ocean), presented a greater diversity of cnidae types compared to specimens from the Pacific Ocean (Table 1). Furthermore, there was also a high variation in the size of cnidae in the Brazilian populations, which were larger, on average.

Comparison with other locations. The size, tubercle distribution, coloration, number of mesenteries, and tentacles of the polyps in this study were within the variability previously recorded for *I. tuberculatus* sensu lato (Table 1). The fluorescent colony collected in Serrambi was more distinct, but still within the previously known range of variation. In contrast, the cnidom was more diverse and had greater average sizes when compared to the specimens from the Pacific Ocean. Unfortunately, there are no cnidom data for the other Caribbean material (previously described as *I. duchassaingi*) to allow for a comparison.

Duerden (1900) noted that Carlgren (1896), when describing representatives of *Isaurus*, discovered that as a rule, the smooth concave part of the column corresponds to the dorsal side of the polyp. However, in the description of the *I. duchassaingi* specimens from Porto Rico, this pattern was not verified, as tubercles were also observed on the dorsal side (Duerden 1900). In the material from the Brazilian coast, two patterns occurred. In some polyps, the smooth concave part was observed without tubercles, coinciding with the dorsal part of the polyp. However, in the same colony, other polyps had tubercles around the whole column, with only the most proximal part of the polyp being smooth. Juvenile polyps and those on the lower part of the colony, which were covered by other polyps, were generally smooth or with non-prominent tubercles. More exposed polyps were covered by algae and had large tubercles on the convex surface, facing "upwards". Whereas more erect polyps commonly presented tubercles around the whole column.

Distribution of *I. tuberculatus* in the western South Atlantic (Fig. 1). Grohmann and Peixinho (1995) reported *I. tuberculatus* in the South Atlantic based on specimens collected in Bahia, northeastern Brazil. However, Laborel (1870) had previously reported this species

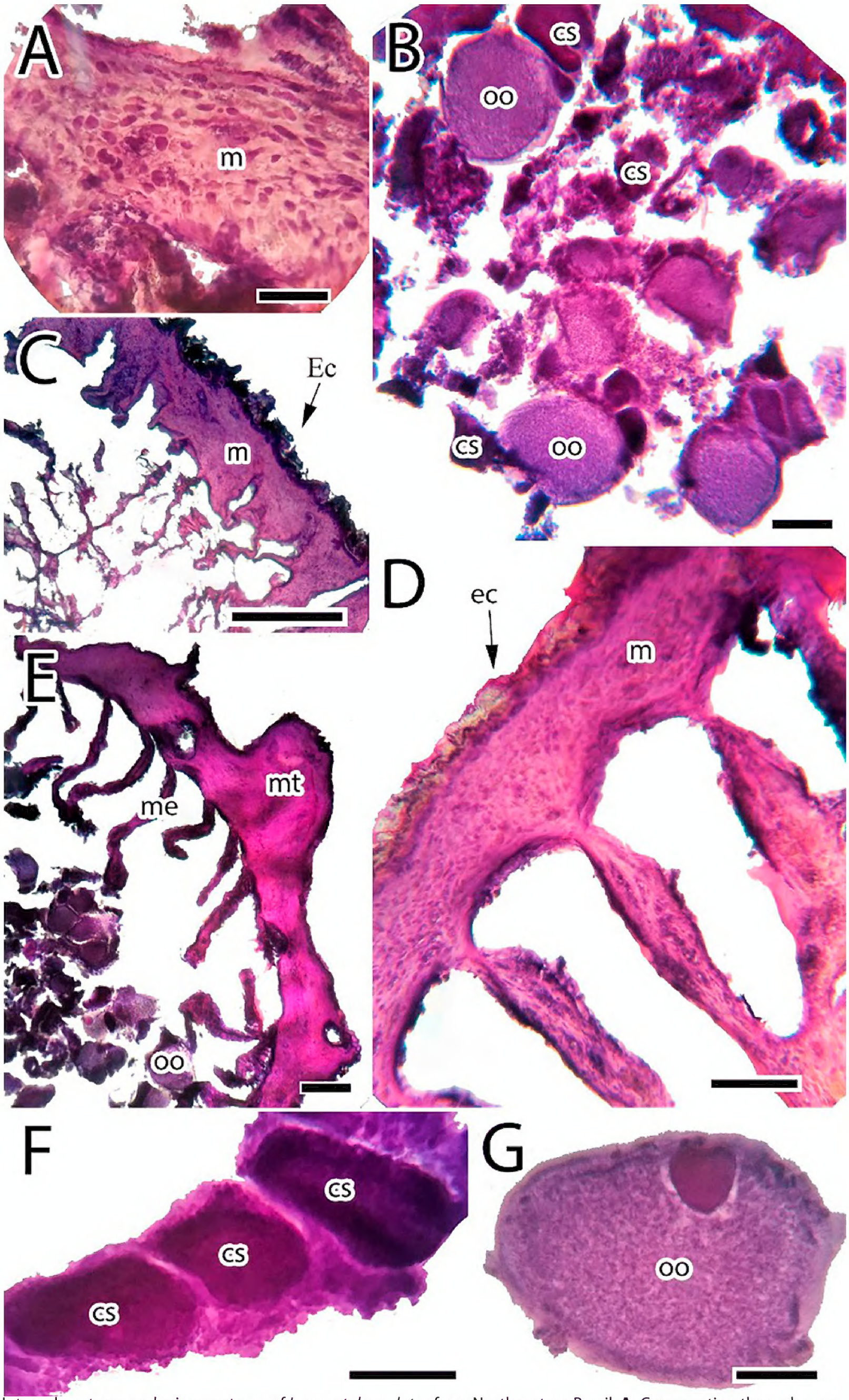

Figure 3. Internal anatomy and microanatomy of *Isaurus tuberculatus* from Northeastern Brazil. **A.** Cross section through scapus showing the thick mesoglea. **B.** Cross section of a fertile specimen showing oocytes and spermatic cysts. **C.** Detail of the proximal scapus. **D.** Cross section of the scapus showing the mesoglea thicker than ectoderm. **E.** Cross section of the scapus through a tubercle showing the thicker mesoglea. **F.** Detail of a fertile mesentery showing spermatic cysts. **G.** Detail of a mature oocyte. Abbreviations: m = mesoglea; oo = oocyte; cs = spermatic cyst; ec = ectoderm; mt = mesoglea adjacent to the tubercle; me = mesentery. Scale bars: A, B, F = 100 µm; C = 500 µm; D, E = 200 µm; G = 50 µm.

at Cabo de Santo Agostinho (Suape and Gaibu) in Pernambuco (as *Isaurus* sp. cf. *I. tuberculatus*). This species was later recorded in Ceará (Morandini et al. 2006; Rabelo and Matthews-Cascon 2007; Soares et al. 2011). More recently, Gondim et al. (2020) reviewed material deposited in the zoological collection at the Federal University of Paraíba (UFPB) and listed *I. tuberculatus* from several locations in Northeastern Brazil (Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, and Bahia). None of these studies provided a complete description of the material. Only the the external morphology of the samples from Bahia were described (Grohmann and Peixinho 2005). Ratto and Castro (1994) presented an abstract at the Brazilian Zoology Conference, in which they described the morphology and microanatomy of *I. tuberculatus* from Ceará (Cabo de Itarema), Rio Grande do Norte (Peroba, Timbau do Sul, Ponta de Cibaúma, Baía Formosa, Cabo do Bocopari), Pernambuco (Ponta de Serrambi, Ponta do Sirinhaém, Praia de Atalaia in Fernando de Noronha), and Bahia (Itaparica Island, Morro de São Paulo, Santa Cruz de Cabrália, Abrolhos). Unfortunately, this research was never published, and the abstract contained very little information. An unidentified species of *Isaurus* has also been reported for the archipelago of Fernando de Noronha (Pires et al. 1992), which Ratto and Castro (1994) considered to be *I. tuberculatus*. However, Santos et al. (2019) thought *I. tuberculatus* to be absent in Fernando de Noronha, although Santos et al. (2016), in their review of the order Zoantharia in Brazil, cited *I. tuberculatus* from the archipelago, although failed to record its presence in the coastal zone of Pernambuco (Laborel 1970). This article increases the distribution of *I. tuberculatus* in other locations and updates the distribution previously registered for the species along the Brazilian coast (Fig.1).

Discussion

If all the synonyms proposed and accepted so far are considered, *Isaurus tuberculatus* sensu lato, is possibly the most widely distributed zooxanthellate zoantharian species. It has been recorded in the western Atlantic from Bahia, Brazil (13°S), to Bermuda (30°N). It occurs at several oceanic islands in the Atlantic, from Santa Helena (15-16°S) to the Canary Islands (28°N). The absence of records of *I. tuberculatus* along the west coast of Africa is likely due to the lack of studies in this area; this region has the largest knowledge gap for the order Zoantharia in the Atlantic (Santos et al. 2019). In the Indian and Indo-Pacific Oceans, *I. tuberculatus* is also widely distributed in tropical and subtropical regions, occurring off the east coast of South Africa west to southern Asia and Australia, and north to Kochi, Japan (32°30'N).

The wide distribution of this species could be a result of its extended larval stage. Although there are no data on *I. tuberculatus* larvae, some representatives of the suborder Brachycnemina have Zoanthinae larvae with long planktonic lifespans (Polak et al. 2011). However, no larvae of Zoanthidae have been collected in waters with temperatures lower than 18 °C (Ryland et al. 2000), which may limit their dispersion. Additionally, it is common to have sister species in the Pacific and Atlantic, partly explained by the recent closing of the Isthmus of Panama (Reimer et al. 2012). However, there are no other zoantharian species nor zooxanthellate coral that inhabit both the Atlantic and Indo-Pacific (Reimer et al. 2012). All the Brazilian populations were in shallow reef areas (<2 m), the majority of which were intertidal. Although *I. tuberculatus* has been reported at depths of 15–20 m in the Caribbean (Larson and Larson 1982; Montenegro et al. 2020), other species of *Isaurus* are commonly found at shallower depths (Reimer et al. 2008).

In the current classification, *I. tuberculatus* is the single valid species of the genus present in the Atlantic Ocean. Along the coast of the Americas, the species occurs widely from Central America and the Caribbean, whereas in Brazil it is limited to the northeastern coast of the country. Although other zoantharians of the family Zoanthidae, such as *Zoanthus* species, occurs south to São Paulo (23°S) (Santos et al. 2016), the most southern record of *I. tuberculatus* is at Pituba, Bahia (13°S) (Grohmann and Peixinho 1995). This confirms the tropical distribution of the genus and the absence of *I. tuberculatus* at less than tropical temperatures (Reimer et al. 2008a). At most tropical Brazilian oceanic islands, includinging the São Pedro and São Paulo Archipelago, Atol das Rocas, Trindade, and Martim Vaz, *I. tuberculatus* has not been found (Echeverría et al. 1997; Amaral et al. 2002; Santos et al. 2020). This could be due to its cryptic habit, since this species has a similar coloration to its surrounding background (gray, brown, cream, green), in addition to its limited abundance in some of its areas of occurrence (e.g., Japan: Reimer et al. 2011a; Brazil: present study). Conversely, the quantity of records of *I. tuberculatus* in various locations in recent decades, suggests that even with small colonies, this species appears to be common and widely distributed. This is confirmed by the number of records of the species (>60) from several localities on citizen science sites such as iNaturalist (https://www.inaturalist.org/).

The analyzed Brazilian samples presented variations in external morphology, especially in size, coloration, and distribution of tubercles, but these are within the range reported for *I. tubercualtus* sensu lato and also within the range of variation observed in samples of *I. tuberculatus* sensu stricto (excluding synonyms such as *I. duchassaingi*, *I. assymetricus*, *I. spongiosus*, and *I. elongatus*). Green-gray and brown/cream polyps similar to the colonies in northeastern Brazil are known from several locations such as the east coast of Africa (Ortiz and Lalana 1988 as *I. duchassaingi*; Branch 2017 as *I. spongiosus*), Santa Helena (Santos et al. 2019), Fiji, and Australia (Muirhead and Ryland 1985). The fluorescent green pattern observed in Serrambi is also known in Japan, where the color of colonies (white, red, purple, or gray) is associated with the environment (Reimer 2007).

The high morphological plasticity of this species, mainly in coloration and size, has been discussed in detail by Larson and Larson (1982), Muirhead and Ryland (1985), and Reimer et al. (2008b). Cluster size and the presence or absence of coenenchyma connecting the polys are variable in *I. tuberculatus*. In Belize (as with *I. duchassaingi*), some clusters reach 700 polyps with clumps of more than 100 individuals. However, smaller clusters are more common, as observed in Brazil.

Microanatomical aspects such as mesoglea thickness and the number of mesenteries were more homogenous in our studied populations, but too few specimens may have been studied. These characteristics also present inter-populational variation worldwide (see Reimer et al. 2008b). The cnidom of our study populations were more diverse and were larger than previous descriptions. Herberts (1972) and Muirhead and Ryland (1985) stated that the size of the cnidom is uniform within a genus and does not serve to distinguish species. However, our observation highlights the necessity of observing this characteristic more closely. Unfortunately, few complete published descriptions of the cnidom of *I. tuberculatus* populations exist, and our data is the first for South Atlantic populations.

The presence of tubercles in the polyp column has been considered the main characteristic of this species, permitting its easy recognition. Of the three species recognized in the genus, *I. cliftoni* does not present tubercles, but it shares other characteristics of the genus, such as the absence of incrustations, presence of zooxanthellae, colonial habit, and polyps that may not be connected by stolon (Muirhead and Ryland 1985). The number and arrangement of tubercles contributes to the separation of *I. maculatus* and *I. tuberculatus*. The former has smaller and more numerous tubercles, arranged in circular series without the formation of a differentiated crown between the capitulum and scapus, which is the opposite in *I. tuberculatus* (Muirhead and Ryland 1985; Thakkar et al. 2018). Although this was confirmed in our Brazilian material and in the population descriptions of *I. tuberculatus* around the world, the high intraspecific variation of this characteristic should be noted. Some *I. tuberculatus* juvenile specimens may not have tubercles and present a smooth column instead (e.g., Japan: Reimer 2007; Porto Rico: Duerden 1900; Brazil: this study). The tubercle crown may be absent or indistinguishable (Larson and Larson 1982; Brazil: this study), and the number and distribution of tubercles can vary, being exclusively present on the convex side of the polyp or also on the concave side, with a varying quantity in each row (Khushali et al. 2014). The variation within the same cluster found in the Brazilian populations suggests that the formation, size, and distribution of tubercles are more related to local environmental conditions at a micro scale. Short-term studies (<10 days) in aquaria, revealed a loss in coloration and reduction in tubercles in *I. tuberculatus* individuals kept in the dark, with a posterior recuperation after exposure to light. This high intraspecific plasticity can represent a greater adaptive ability to changes in the environment (Todd 2008), which likely contributes to the wide distribution of *I. tuberculatus*.

The first reproductive data for this species were provided by Duchassaing de Fonbressin and Michelotti (1860), revealing the presence of female gametes. Later, in material from Bermuda, McMurrich (1889) found hermaphroditic polyps. Other authors also described the distribution of gametes in mesenteries in species now synonymous with *I. tuberculatus* (e.g., *I. duchassaingi* in Belize: Larson and Larson 1982), describing polyps with only female gametes and hermaphroditic polyps. However, many studies found no gametes (e.g. Varela et al. 2002; Khushali et al. 2014; Thakkar et al. 2018). Among the populations we studied, only Porto de Galinhas colonies presented gametes (oocytes and spermatic cysts), with hermaphroditic polyps. The small quantity of fertile colonies in this species may suggest a dominance of asexual reproduction, which has its focus on maintenance of colonies and the local population. This was observed in populations in Belize (identified as *I. duchassaingi*), which formed numerous clusters (Larson and Larson 1982). For some *Zoanthus* species (closely related to *Isaurus*), the increase in colony fragmentation and clone production is associated with a low level of recruitment and larval dispersion in the reefs of South Africa (Ryland 2015). The investment of *I. tuberculatus* in asexual reproduction may explain the formation of its colonies but does not explain the supposed pantropical distribution without high larval production. In addition to the dispersal of larva, the adult phase may be dispersed on natural or artificial floating objects. *Isaurus tuberculatus* was found attached to a nylon mooring line in Palau (Santos and Reimer 2018) and may be dispersed by rafting. However, temperate and cold waters beyond the limitations of this species' tolerance may be a barrier and may restrict is successful dispersal (Reimer et al. 2008a).

Approaches using zooxanthellae may help to identify cryptic species and to delimit species (Risi and Macdonald 2015). However, populations of *I. tuberculatus* in Japan, Cape Verde Islands, and West Africa (Reimer 2008b; Reimer et al. 2011a; Risi 2014; Risi and Macdonald 2015) present Symbiodinaceae of the subclades C1/C3 (currently *Cladocopium*). Several species in this group are highly generalist and are also found in other zoantharian genera (Reimer et al. 2008b).

South Atlantic populations *I. tuberculatus* coincide with descriptions of specimens from the Indo-Pacific, identified as *I. tuberculatus*, but also with Caribbean specimens described originally as *I. duchassangi*, a species that was reported in many locations throughout the Caribbean until it was synonymized with *I. tuberculatus*. According to Larson and Larson (1982), *I. duchassaingi* shows much variation in the size, coloration, and number of polyps in clusters, as well as tubercle distribution and microanatomical aspects. Similar variation has been noted in Indo-Pacific populations (especially from Japan)

of *I. tuberculatus* sensu stricto (Reimer et al. 2008b) and in *I. tuberculatus* sensu lato (including *I. elongatus*, *I. assymetricus*, and *I. spongiousus*; Muirhead and Ryland 1985). As such, western South Atlantic populations can certainly be identified as *I. tuberculatus*, but it is not possible, using morphology, to determine if they are closer to Caribbean populations previously identified as *I. duchassaingi* or with Indo-Pacific populations.

The co-specificity between Atlantic and Indo-Pacific populations has been questioned by various authors (Reimer et al. 2008a; Montenegro et al. 2020). As previously discussed, the elevated variability within clusters and between populations, both in the Atlantic (confirmed in this present study) and in the Indo-Pacific does not permit the separation of species. Until now, molecular studies with populations in Florida, Cape Verde Islands, Saint Helena, and West Africa found congruence between the sequences collected and the *I. tuberculatus* populations in Japan (Reimer et al. 2010, 2012; Risi and Macdonald 2015; Santos et al. 2019). However, results differed according to the molecular marker used, and although the molecular analyses indicated co-specificity, the authors of these studies acknowledged the improbability of this based on the absence of a zooxanthellate species inhabiting the Atlantic and Indo-Pacific. The material from Japan has been used as a reference for the species, used to confirm the identification of material collected elsewhere. Unfortunately, Guadaloupe (the type locatity of *I. duchassaingi*), other Caribbean, and South Atlantic samples have not been included in any molecular study. For *I. tuberculatus*, the type locality is unknown and there has never been a redescription of the holotype. If *I. tuberculatus* sensu lato is determined to be a species complex, it will be important to consider the characteristics of the type material in order to describe the taxonomic entity that will carry the binomial.

With the morphological data presented here, it is not possible to determine whether the populations of the South Atlantic are closer to the populations of the Caribbean (previously described as *I. duchassaingi*) or with those of the Indo-Pacific (described as *I. tuberculatus*). Nevertheless, considering the great variability found in this study and already recorded for this species and the absence of zoantharian zooxanthellae distributed throughout the three oceans, we suggest that Atlantic populations are distinct from the Indo-Pacific populations. Perhaps *I. duchassaingi* should be reinstituted to group these populations, or maybe more than one species exists in the Atlantic. A revision of the genus is urgently required, with microanatomical descriptions and a molecular analysis using fast-evolving markers from a large number of populations throughout the purported geographic distribution of the species. Until this has been done, to avoid increasing the number of synonyms and nominal taxa in the genus, we prefer to maintain the Brazilian populations as *I. tuberculatus* in the broadest sense.

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Authors' Contributions

Conceptualization: CP, PBG, ÉPL. Data curation: CP. Formal analysis: ÉPL, DVN. Supervision: PBG. Validation: PBG. Writing – original draft: DVN, ÉPL. Writing – review and editing: CP, PBG.

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